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DIMORPHIC QUEENS IN AN AMERICAN ANT (LASIUS LATIPES WALSH).[1]

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On the afternoon of September 17 of the current year the senior author had occasion to witness the nuptial flights of several species of *Lasius* in an open wood near Rockford, Illinois. These flights occurred almost simultaneously from mound nests of *Lasius niger* var. *americanus*, *L. claviger* and *L. latipes*. The first species is ubiquitous in all open country in the Northern States, especially where the soil is sandy or loamy. Owing to the dingy color of the workers, males and females, and the relatively small size of the colonies, the nuptial flight of this species offers nothing of special interest or beauty. It is quite otherwise with some of the yellow *Lasius*, [illegible] species are known to occur in the United States, namely: *L. aphidicola* Walsh, *speculiventris* Emery, *brevicornis* Emery, *myops* Forel, *interjectus* Mayr, *claviger* Roger, *latipes* Walsh, and *Murphyi* Forel. The last is known only from North Carolina and Colorado. *L. interjectus*, *aphidicola*, *claviger* and *latipes* build large mound nests, often a foot or more in diameter and several inches high, either in open grassy places or about the bases of rotting stumps. These mounds are shot through with living grass and covered with little openings for the ingress and egress of the ants. *L. latipes* in some localities prefers to build its nests under rather large stones. This is the case at Colebrook, Connecticut, for example. Unlike *L. niger* and its varieties the yellow species of the genus appear to be nocturnal in their habits and *L. myops* largely subterranean. At any rate the workers of these various species are not seen to leave the nests in the day-time except during the nuptial flight of the males and virgin females.

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[1] Contributions from the Zoölogical Laboratory of the University of Texas, No. 46.

This flight, especially in the case of *L. latipes*, presents a beautiful spectacle. At the moment when the great swarming impulse seizes the colony, the shining amber-yellow workers, together with the hosts of sable males and large tawny-red females, break in a flood from the main openings of the nest.

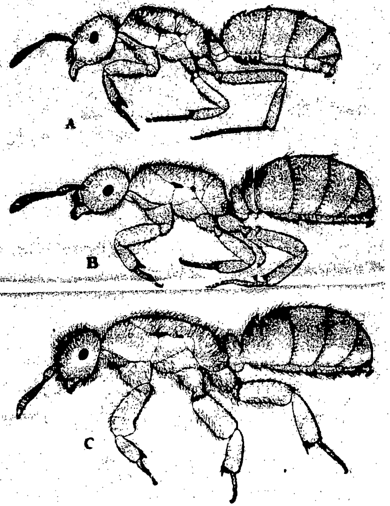

FIG. 1. *A*, *Lasius claviger* Roger ♀; *B*, *Lasius latipes* Walsh α-♀; *C*, *L. latipes* β ♀. The wings are omitted.

The winged forms hasten up the slender grass-blades on which they rock for a few moments, while filling their tracheæ with the pure air of the upper world, then one by one spread their glittering wings and soar into the air like sparks rising from a fire.

While watching a colony during this interesting culmination of its annual development, the senior author noticed females of two different kinds issuing in numbers from the same openings of the grass-covered mound. The majority of these females were the remarkably pilose individuals, of a rich fulvous red, with extremely broad and flat legs and abnormally short, feeble tarsi, which have always been regarded as the true females of *L. latipes*. Among these, however, there were several hundred females which were perceptibly smaller, of a deep brown color, much less pilose, with only moderately broadened and compressed legs and with much longer tarsi. Both forms mingled with the workers and males and took flight together within the same half hour. Although the unusual character of this observation was fully appreciated at the time, circumstances made it impossible to excavate the nest and search its penetralia for the mothers of these very different virgin females. It seemed best to leave the nest for careful study at some future time and to collect a large number of the workers, males and females at the surface.

In this paper we will designate as the β-female the highly aberrant form (Fig. 1, *C*) with the excessively flattened legs, *i. e.*, the form which has hitherto passed as the true and only female of *latipes*; the other (Fig. 1, *B*) we will call the α-female. These designations will suffice for present purposes and will leave the facts uncolored by the conjectural meaning of this singular dimorphism.

A few days after the above recorded observations were made the senior author returned to Texas, and soon afterwards, with the aid of the junior author, undertook an examination of all the material of *L. latipes* collected during three consecutive summers in three different localities. This was easily possible because the specimens from different nests had been kept by themselves in separate vials of alcohol. There were, in all, collections from ten separate nests, as recorded with the date of capture and the personnel of each colony in the following table:

Nest No. 1. Woods Hole, Mass., Aug., 1900. ☿, ♂, β-♀.
Nest No. 2. Woods Hole, Mass., Aug., 1900. ☿, β-♀.

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	L. claviger. ♀*	L. latipes. α-♀	L. latipes. β-♀
Length of thorax	2,517	3,390	3,487
Length of gaster	3,055	3,681	3,487
Length of petiole	285	303	392
Height of petiole	872	926	943
Length of antennal scape	926	890	854
Apical breadth of antennal scape	178	230	267
Length of funiculus	1,566	1,513	1,370
Breadth of funiculus	214	231	249
Length of fore femur	1,246	1,264	1,335
Length of middle femur	1,193	1,175	1,282
Length of hind femur	1,356	1,388	1,460
Breadth of fore femur	427	498	659
Breadth of middle femur	303	427	605
Breadth of hind femur	356	463	623
Length of fore tibia	1,068	1,015	979
Length of middle tibia	1,015	1,050	1,086
Length of hind tibia	1,513	1,513	1,442
Breadth of fore tibia	320	356	445
Breadth of middle tibia	267	338	427
Breadth of hind tibia	267	356	481
Length of fore spur (strigil)	338	320	231
Length of middle spur	231	249	249
Length of hind spur	267	267	267
Length of whole fore tarsus	1,015	905	729
Length of first fore tarsal joint	570	518	374
Length of second fore tarsal joint	89	89	89
Length of third fore tarsal joint	89	71	71
Length of fourth fore tarsal joint	89	71	53
Length of fifth fore tarsal joint	178	160	142
Length of whole middle tarsus	1,175	961	818
Length of first middle tarsal joint	606	534	409
Length of second middle tarsal joint	125	107	89
Length of third middle tarsal joint	107	89	85
Length of fourth middle tarsal joint	107	89	71
Length of fifth middle tarsal joint	231	142	160
Length of whole hind tarsus	1,691	1,406	997
Length of first hind tarsal joint	872	783	570
Length of second hind tarsal joint	[illegible]	160	107
Length of third hind tarsal joint	142	125	89
Length of fourth hind tarsal joint	107	89	71
Length of fifth hind tarsal joint	267	249	160

signed to the limbo of useless specific diagnoses except for the mention of the extraordinarily flattened legs in the female, a character which is, moreover, emphasized in the specific name. Walsh had only two specimens of the β-female. The locality of the types is not given, but was probably Rock Island, Illinois. It was the flattening of the legs of *L. claviger*, a trait still more pronounced in *latipes* and visible also in *interjectus* and the more recently discovered *Murphyi* that led Mayr ('62, p. 51) to separate these forms as the genus *Acanthomyops*. Later he reduced this genus to subgeneric rank under *Lasius*, where it is still used to include those species which have 3- instead of 6-jointed maxillary palpi. Mayr redescribed (**'66,** p. 889) the β-female from a defective specimen from Wisconsin, and says that he was at first tempted to place it in a new genus on account of its remarkable appearance. That he refrained from doing this is evidence of his keen taxonomic insight. Later writers, like Emery (**'93,** p. 638), have included the β-female in the table of *Lasius* species as distinguishable from all other females by having "the hind tarsus shorter than the much flattened tibia." The discovery of the α-female, which has the hind tarsus longer and the tibia much less dilated, makes it more difficult to recognize the species. This has induced us to make a closer study of *L. latipes* and of the allied *claviger* in all the sexual phases.

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* The dimensions are in micra.

Comparison shows that the α-female is almost intermediate between the β-female and the female of *claviger*. This is clearly shown in the figures, in the table of measurements on p. 153, drawn up by the junior author, and in the two-column statement of the principal differences between the α- and β-females, as compared with the female of *L. claviger* as a standard:

α-female of Lasius latipes.	β-female of Lasius latipes.
1. Dark brown, like *L. claviger* ♀.	1. Fulvous red, in one nest (No. 5) dark brown like the α-female.
2. A little more pilose and pubescent than *L. claviger* ♀.	2. Much more pilose and pubescent.
3. A little larger.	3. Considerably larger and longer.
4. Thorax longer in proportion to the gaster	4. Thorax much longer in proportion to the gaster.
5. Mesonotum and scutellum as in *claviger* ♀.	5. Mesonotum and scutellum flatter.
6. Petiole thicker, higher and more rounded above than in *claviger* ♀.	6. Petiole considerably thicker, higher and more rounded above.
7. Mandibles similar to those of *claviger* ♀.	7. Mandibles with fewer teeth than in *claviger* ♀ (Fig. 3*C*).

8. Antennal scape and funiculus shorter and broader. (Fig. 2, *B*.)	8. Antennal scape and funiculus still shorter and broader. (Fig. 2, *C*).

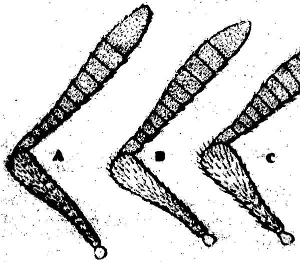

FIG. 2. *A*, Antenna of *Lasius claviger* ♀; *B*, of *L. latipes* α-♀; *C*, of β-♀.

9. Trochanters, femora and tibiæ broader and more flattened.	9. These joints extraordinarily flattened and dilated.
10. Strigil a little smaller.	10. Strigil much smaller.

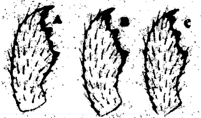

FIG. 3. *A*, Mandible of *Lasius claviger* ♀; *B*, of *L. latipes* α-♀; *C*, of β-♀.

11. All the tarsi a little more tapering.	11. Tarsi rapidly tapering.
12. Middle and hind tarsi nearly as long as the tibiæ.	12. Middle and hind tarsi much shorter than the tibiæ.

Turning now to a comparison of the two species, *latipes* and *claviger*, as exhibited by the workers and males, we find but few points of difference, so that we are compelled to regard the two species as very closely related to each other. The worker *latipes* has a thicker petiole, which is distinctly blunt and rounded above, and the hairs are somewhat more abundant and evenly distributed on the dorsal surface of the gaster. In the worker *claviger*, on the other hand, the petiole is thinner anteroposteriorly and sharply cuneate above when seen in profile, and the gaster is less uniformly hairy and somewhat more shining. The males of the two species differ much as do the workers in the shape of the petiole. Moreover the male *claviger* is decidedly larger, more robust and blacker than the male of *latipes*. These differences, especially in the males, are easily appreciated in the living specimens when they are seen in numbers, but are necessarily more obscure in dried cabinet specimens.

From these comparatively slight differences between the males and workers of the two species we should naturally expect to find a corresponding similarity in the females. It is quite obvious that the α-female is the very form which satisfies this requirement, whereas the β-female presents extreme characters which make it appear like a decided sport or aberration from the normal type of *Lasius* female. It would seem, therefore, that the β-female is the one for which we are most in need of an explanation, although it is connected with the females of normal form by a rather complete series of gradations, *i. e.*, through the females of the following species, beginning with the most extreme form: *L. Murphyi*, α-female of *latipes*, *claviger*, *interjectus*. The remarkable configuration of the legs and antennæ, the color and pilosity of the β-female all suggest some peculiarity of habit or habitat the nature of which remains to be determined by further observation and experiment.

We come now to the important question: What is the meaning of this dimorphism in the females of *L. latipes?* From the fragmentary data at our command it would seem that four different hypotheses might be advanced to explain this peculiar phenomenon:

1. It may be suggested that the α- and β-females really belong to two distinct species. According to this view the α-female might be regarded as the true queen of *latipes*, whereas the

β-form would represent the queen of some inquiline or symbiotic species. Although this explanation is readily suggested by the well-known cases of dulosis and xenobiosis in ants, we are, nevertheless, bound to reject it for the following reasons: Though the β-females were taken in several nests and, in one case, were seen to celebrate their nuptial flight at the very same time as the α-females, no males or workers which could represent any species except *latipes* were to be found in the nests. The same argument would hold *mutatis mutandis*, were we to consider the β-form as the only true female of *latipes*. The workers and males of all the known North American Lasii have been accounted for, and there is still a female form left over, so that there is no species known that could be enslaved by, or live as an inquiline with, *L. latipes*. We should have to suppose that the inquiline species was represented by females only, and this is most improbable. Finally, the deep coloration above noted as occurring in the β-females of nest No. 5 would indicate that both the α- and β-females belong to the same species. We believe, therefore, that this hypothesis may be safely rejected.

2. It may be suggested that the α-female is the normal female of *latipes*, whereas the β-females are diseased forms — individuals afflicted with some strange emmet elephantiasis or acromegaly! But even apart from the very frequent occurrence and uniform development of the β-females, dissection shows that such a view cannot be seriously entertained. Their internal structure is in no respect abnormal. The fat body is well developed and the ovaries are in the same stage and have the same normal structure as the ovaries of the α-females. If anything, the β-females are more vigorous, somewhat larger and supplied with more fatty tissue (even in the distal lobes of the large fore femora!) than the α-females. In a word, the β-females are somewhat above normal, while the α-females, so far as we are able to judge, are quite normal. Hence this hypothesis, also, may be safely rejected.

3. The dimorphism may be regarded as the result of hybridism between *L. claviger* and *L. latipes*. This view is supported by the following considerations:

(*a*) Both species occur in the very same localities, and *latipes* is much rarer than *claviger*. Hence the queens of the latter may find cross-fertilization by males of their own species from other nests very difficult and fertilization by males of *claviger* a relatively easy matter.

(*b*) The nuptial flights of the two species may occur simultaneously. In fact, the senior author witnessed a flight of *claviger* from a nest not twenty feet away from the *latipes* nest and at the very same time (5.30 P. M.) as the above-described flight of the latter species. And it may also be stated that both these nests were large and must therefore have existed side by side for some years. We could suppose that a β-female of *latipes* in some previous year had been fertilized during her nuptial flight by a male *claviger* and had returned into the parental nest to give birth to the α-females which celebrated their nuptial flight on the 17th of September, 1902.

(*c*) This view is also supported by the fact that the α-female is so clearly intermediate in nearly all its characters between the female *claviger* and the β-female, as has been shown in the above tables.

The arguments that can be brought to bear against the hypothesis are the following:

(*a*) We have failed to find any hybrid workers in the nests containing the α- and β-females. This should be the case unless we suppose that all the hybridized β-females produced only queens.[1] But it must be borne in mind that the hybrid between the worker *claviger* and worker *latipes* would differ presumably from the parent species only in intermediate pilosity and in having a petiole intermediate in shape. Such differences would not be easily detected, as anybody will confess who has examined a large series of workers of the two species. The workers are of small size and the petiole is sometimes decidedly variable even within the limits of the same species of *Lasius*.

(*b*) It is improbable that hybridization could occur so frequently in a state of nature as appears to be indicated by the high percentage of nests containing α-females and their occurrence in such widely separated localities. If we are really confronted by a case of hybridism we are almost compelled to believe that the *α*-female must be sterile, notwithstanding her well-developed ovaries, or the two species would long since have merged into one.[1]

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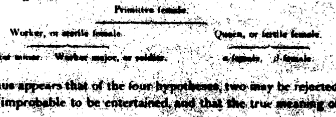
[1] Obviously the male offspring of the hybridized queen would not be affected, since they arise from unfertilized eggs.

(*c*) It seems improbable that such an aberrant creature as the *β*-female would mate with the male of another species, but this argument loses much of its force when we stop to reflect that the *claviger* male is very similar to the *latipes* male even in the structure of its genitalia.[2]

4. We may suppose that we are dealing with a true case of dimorphism in the female sex. On first thought this seems improbable because dimorphic queens, in the strict sense of the term, are unknown among ants. But when we stop to consider that the social bees and wasps exhibit an essentially similar dimorphism, except that one of the two winged forms, the worker, is sterile (and this may also be the case with the *α*-female of *L. latipes* !) there is nothing preposterous in this view. Moreover, in ants the wingless workers have themselves in many species become dimorphic, developing soldier and typical worker forms, either perfectly distinct from each other or connected by a series of intermediates. Why, then, may we not expect the winged queens in some cases to exhibit dimorphism among themselves, especially when dimorphism "runs in the blood," so to speak, of all the social Hymenoptera? And why may not *L. latipes* be such a species in which the old and deeply-rooted tendency is breaking out in a novel form? This would at least complete the theoretical possibilities in female ants as represented in the following diagram:


Primitive female.
Worker, or sterile female.
Queen, or fertile female.
Worker minor.
Worker major, or soldier.
α-female.
β-female.

It thus appears that of the four hypotheses, two may be rejected as too improbable to be entertained, and that the true meaning of the dimorphism of the females of *L. latipes* is to be sought in the direction of hybridism or of dimorphism *sensu stricto*. Only further observation and especially experiment can enable us to decide which of these interesting alternatives confronts us.[1]

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[1] Unless, indeed, the Mendelian law be supposed to operate with unprecedented clearness in this particular case.

[2] In this connection, however, it is interesting to note that Marchal ('96, p. 45) failed to induce mating between two very closely allied species of wasp (*Vespa germanica* and *V. vulgaris*).

For the present we incline to the belief that the *a*- and *β*-females of *latipes* represent true dimorphic forms, and see in this condition an interesting repetition of what may have led to the differentiation of the primitive winged female ant into workers and queens. It is granted on all sides that insects like the ants, social wasps and bees, which present three sexual phases, viz., males, queens and workers, are to be derived from forms with only a single female form. In the bees and wasps there can be no question that this original female form was winged like the male, and we should expect this to be the case also with the ants, but so eminent a myrmecologist as Professor Emery takes quite a different view of the matter ('95*b*, p. 775). He says: "If the above considered derivation of ants from Mutillid-like Hymenoptera be granted, we must suppose, furthermore, that in primitive ants, as in the Mutillids, the males were winged, but the females wingless, and that the latter subsequently reacquired wings. This supposition is upheld by the fact that wingless females are most commonly met with among the Dorylinæ and Ponerinæ, *i. e.*, in those very groups of ants which are the most primitive, more rarely among the Myrmicinæ, and most rarely, and, so far as I am aware, only as individual anomalies, in the Dolichoderinæ and Camponotinæ. The frequency of occurrence of wingless females is, therefore, inversely as the phyletic stage of development of the different groups of ants.

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[1] In the Lepidoptera and Hymenoptera, if we except a few cases like the Torymid Chalcididæ, the female sex seems to be more prone to dimorphism than the male. In Diptera the few recorded cases of dimorphism occur in males; *e. g.*, in the Brazilian *Curupira torrentium* (Fritz Mueller, '81; Osten Sacken, '95) and the North American Syrphid *Mallota cimbiciformis* (Williston, '86). Among the Coleoptera *Dytiscus* presents dimorphism in the females, while some of the Anthribidæ are said to show it in the males. The dimorphism seen in the "high" and "low" males of the Scarabæidæ among the Coleoptera and the "high" and "low" male Dermaptera (*Forficula auricularia*) observed by Bateson ('94, pp. 40–42), resembles that of the female *Lasius latipes* in being a normal and excess development of the individuals of the same sex. In the latter case, however, the two forms are not connected by intermediate variations.

"Not only is the normal occurrence of wingless females among existing species evidence of a similar condition among the primitive ants, but it also furnishes the most natural explanation of the origin of the wingless workers. I surmise that *the ancestral ants constituted small societies of wingless females, among which sterile individuals were subsequently differentiated as workers.* The wings, so readily deciduous in the queens of existing ants, were newly acquired from rudiments still persisting in the ontogeny, by a process of reversion to the winged ancestors."

We are unable to assent to this view, for the following reasons:

1. While there is no end of evidence to show that the most diverse insects have lost their wings during phylogeny, there is not, to our knowledge, a single insect which can be satisfactorily shown to have reacquired these organs. At any rate the losing of wings is a much easier process than their acquisition.[1] Emery's hypothesis postulates a winged condition in both sexes of the ancestors of Mutillidæ, a loss of the wings in the females of the Mutillid-like ancestors of ants, a persistence of this primitive condition by inheritance in the ancestral Formicidæ and a comparatively recent reacquisition of wings in the females of all except the Dorylinæ and the few Ponerinæ genera which have wingless females (*Leptogenys, Acanthostichus*). This would seem to be a needless complication of matters, apart from the fact that it is venturesome to invoke the obscure principle of reversion to account for the reacquisition of organs.

2. Existing wasps and bees certainly show the possibility of differentiation into workers and queens prior to the loss of wings,

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[1] This is an interesting case of a principle to which Headley ('01, pp. 100, 101) has recently called attention: "The sudden loss of horns brings out a point to which, I think, attention has never been directed in discussions on panmixia. The evolution of new characters is a gradual process requiring ages of time. Geology shows that the stag's antlers have grown step by step from small beginnings. But they might be completely lost in a single generation. The horns of cattle, though less magnificent, are none the less the slow product of ages of unintermitted selection. But by a sudden freak they disappear utterly in an individual here and there, or leave only a dangling vestige attached to the skin.

"Those evolutionists who love symmetrical theories, mapped out regardless of observed facts, imagine a process of retrogression by which all the stages are retraced in ordered succession. What actually happens is usually very different. An elaborate organ is suddenly much reduced and mutilated or suddenly disappears altogether."

And there is no strong evidence to show that this condition did not exist in the ancestral ants, for the Dorylinæ are hardly in the direct line of Formicid descent, and the Ponerinæ, though very primitive, still show the differentiation into winged queens and wingless workers in some of their most generalized genera (*Cerapachys*, *Sysphincta*, *Proceratium*, etc.).

3. That the most natural way of accounting for the wingless workers is through loss of the organs of flight in one of the two winged female forms, is also indicated by the phenomena of ergatomorphism among male ants. It is known that in a few sporadic species belonging to several genera the males are wingless and have assumed a worker-like form, especially in the development of the thorax. These species are, *Anergates atratulus* (Schenck '52), *Formicoxenus nitidulus* (Adlerz '84), *Cardiocondyla Stambuloffii* (Forel '92), *Ponera punctatissima* (Emery '95a) and *P. ergatandria* (Forel '93). This same reduction of the wings is shown in a more or less advanced condition in some male Mutillidae. All these cases are most naturally explained by loss of the organs of flight, and we are justified in adopting the same explanation to account for the wingless condition of the workers. Our view of the matter, therefore, would differ from Emery's in assuming that in the ancestors of the ants all three forms, workers, queens and males, were alike winged, and that the workers lost their wings either suddenly in accordance with Headley's principle, or concomitantly with the atrophy of the ovaries and the assumption of the other worker characters. Thus it would be the workers that have lost their wings and the queens have not reacquired, but retained these organs which came to them as the common heritage of all the Pterygote insects.

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December 5, 1902.